

# Overview of numerical models of cell types in the cochlear nucleus

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The cochlear nucleus (CN) plays an important role in auditory scene analysis. It is the first center in the auditory pathway and the first stage for cue encoding. Examples for modeled cue extractions are the onset detection, periodicity analysis, monaural reverberation removal, and preprocessing for binaural cue analysis. The studies on the CN have been done incorporating different disciplines, in particular neurobiology and computational neurophysiology. As a result, several types of cells with different response behaviors, interconnections, and connections to other parts of the brain are determined and modeled. One aim of these investigations is to model the auditory processing, which can be used to simulate acoustical phenomena. The number of published contributions about the structure and components of the CN, and their computational models is numerous. Especially the modeling of various cell types, their different cue encoding methods, and their diverse interconnections can increase perplexity. The intention of the authors is to give an insight in numerical models of the cochlea nucleus. For this, a simplified map of the cochlear nucleus with its connections is built up from the literature of the different disciplines. The authors are aware of that this paper cannot give an all-embracing overview of all models and intricacies.

## MOTIVATION AND INTRODUCTION

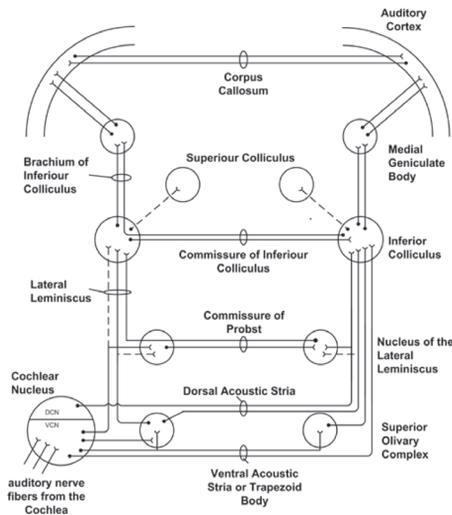
The motivation for this paper is to give an overview about the structure of the cochlear nucleus and a collection of a few exemplary numerical models of cue encoding in the CN. The presented summary can be useful for scientist planning to start research in this field, and for those wanting to get an overview about the different cue encoding of the CN. Publications in this area are reviewed, cross-checked and cited through this paper.

## MAP OF THE COCHLEAR NUCLEUS

The CN is a peripheral nucleus of the central auditory system and the first stage of cue encoding after the organ of Corti (Fig. 1). The auditory nerve fibers (ANFs) from the cochlea are one main input for this nucleus. The ANFs are divided by means of their spontaneous activity into high, middle, and low spontaneous rate (H-, M-, and

LSR, respectively). The several regions of the CN are excited by different types of these ANFs in dependence of the intensity of the sound signal. Non-ANF terminals are from higher regions of the auditory pathway and from outside the auditory system (Ehret and Romand, 1997). Figure 1 shows the ascending auditory pathway for the left side starting with the auditory nerve fibers.

A simplified map of the CN with its divisions, signal flow, and interconnections is shown in Fig. 2 at the end of this chapter. This map was built up from literature, mainly from Ehret and Romand (1997), Oertel and Golding (1997), Oertel and Young (2004), Tzounopoulos *et al.* (2004), and was cross-checked with other literature from computational neurophysiology. Only the distribution of main cell types, the ascending pathway, and no feedback control within the CN are shown in Fig. 2. The convergent inputs from several auditory nerve fibers to the neurons in the AVCN are not presented in Fig. 2 to keep perspicuity of the figure. Only the characteristic input is shown.



**Fig. 1:** Ascending auditory pathway (left pathway). From Ehret and Romand (1997).

## Divisions

The CN is divided into three main regions with a tonotopic like structure. These regions are the rostral and caudal anteroventral part (AVCN), the posteroventral part (PVCN), and the dorsal part of the CN (DCN). The caudal AVCN and the PVCN receive their main inputs from auditory nerve fibers (Ehret and Romand, 1997). The DCN receive inputs from the ANFs and from the so called mossy fibers from other regions of the brain. These inputs convey signals for the head and ear position

(Tzounopoulos *et al.*, 2004), signals from higher stages of the auditory pathway, and from other regions of the brain (Oertel and Young, 2004). The rostral AVCN is further divisible into an anterior and posterior area of the anterior part. The caudal AVCN is divisible into a ventral and dorsal area of the posterior part. The DCN can be anatomically divided into the molecular, pyramidal, and polymorphic cell layer with its dedicated cells (Ehret and Romand, 1997; Oertel and Golding, 1997; Oertel and Young, 2004; Tzounopoulos *et al.*, 2004).

### Cell types

The neurons within the CN can be classified by their response patterns to tone-bursts and by their morphology. Investigations of e.g. cat brain show that generally there are different cell types in different regions of the CN (see Fig. 2).

Spherical bushy cells can be found in the rostral part of the AVCN. They show a response pattern which is very similar to that of auditory nerve fibers. Those neurons are called “primary-like”. They are excited by tonotopic structured ANFs. Their outputs go through the trapezoid body to the nucleus of the lateral lemniscus and to the superior olive complex.

Globular bushy cells and stellate cells can be found in the caudal part of the AVCN. Globular bushy cells show primary-like with notch behavior, which means that there is a short decrease of activity after the sharp onset peak of activity. The onset peak is time-locked to the stimulus onset. They show a high precision on phase locking of the sound signal (Wittig jr., 2004). They achieve excitatory inputs from the tonotopic structured ANFs and inhibitory input from tuberculoventral cells in the DCN. The outputs of these cells are the trapezoid body and periolivary nucleus. The stellate cells in the AVCN show an onset response with weak discharge after the onset of the tone-burst. They are called onset-type 1 (on-1). They are excited by the tonotopic structured ANFs and have inhibitory inputs from tuberculoventral cells in the DCN. The terminals of these cells are located in the lateral lemniscus and inferior colliculus.

The PVCN contains two further cell types. One type is the d-stellate cell, which shows chopper behavior. The envelope of the response pattern is similar to primary-like response, but with multiple peaks separated by periodic time intervals. Oertel and Young (2004) describe that the inhibitory outputs proceed to tuberculoventral cells, pyramidal and giant cells in the DCN and next to this to the periolivary nucleus. The second cell type in the PVCN is the octopus cell, which shows ideal onset (on-i) behavior to stimulus onset. Their axons go to the inferior colliculus and periolivary nucleus.

The tuberculoventral cells in the DCN show chopper and onset-chopper behavior. The inputs are the tonotopic structured ANFs and inhibitory input from d-stellate cells. Their inhibitory outputs go to the caudal part of the AVCN (Ehret and Romand, 1997), and to the pyramidal cells in the second cell layer of the DCN (Oertel and Young, 2004; Oertel and Golding, 1997).

Giant cells in the DCN receive several inhibitory inputs from parts of the DCN and PVCN. They show build-up behavior which means that onset of the tone-burst is suppressed followed by an increase in excitation. The pyramidal cells in the DCN show a very similar response pattern (pauser). The difference is that the suppression starts after the first initial peak. The onset of the stimulus is encoded. Giant and pyramidal cells encode sharp spectral features like notches, which are caused e.g. by the head related transfer function (Oertel and Young, 2004; Wittig jr., 2004). These cells are excited by ANFs and parallel fibers. Several inhibitory inputs are from parts of the PVCN and the non-tonotopic structured circuits of cartwheel and superficial stellate cells in the first cell layer of the DCN (Oertel and Young, 2004; Oertel and Golding, 1997). The output of the pyramidal cells goes to the inferior colliculus and lateral lemniscus (ventral and in minor dorsal).

## MODELING THE COCHLEA NUCLEUS

In this chapter a few selected computational models of the CN are presented. These models or parts of them are assigned to the assumed cue encoding, divisions and cell types of the CN. Please note that this is not a complete line-up.

### Cue encoding in the Cochlea Nucleus

Main acoustical cues which are encoded by the auditory system are the *amplitude modulation* (AM) and *periodicity* of a sound signal. Frisina *et al.* (1990) found that neurons in the VCN encode AM. He and his colleagues identified on-1 and chopper units in the AVCN and on-i units in the PVCN to be specialized for encoding of AM. These cells are tuned to preferred AM frequencies to which they are maximally responsive. Gai and Carney (2008) are compliant with other studies that inhibitory inputs are generally enhancing the synchronization to AM. They assume that most inhibitory interneurons in the CN are synchronized to AM. It seemed that especially the PVCN is a key area for encoding AM (e.g. Gai and Carney, 2008). The d-stellate units seemed to be encoding the mean discharge rates of ANFs and hence the periods of arriving signals, and give a kind of trigger signal to some CN units at higher stages of the auditory pathway. The octopus units in the PVCN are assumed to encode the onsets of a signal and may play an essential role in periodicity encoding (Ehret and Romand, 1997). Next to this, neurons are identified in the AVCN, which receive convergent inputs from auditory nerve fibers with different characteristic frequency (Carney, 1990). These neurons appear to behave like cross-correlators to detect similar patterns of periodicities in frequency channels (Wang and Brown, 1999).

Tuberculoventral cells in the DCN have inhibitory projections to AVCN units. The connected neurons in the DCN and AVCN are excited by auditory nerve fibers with the same characteristic frequency. Experiments show that the inhibitory potentials of DCN cells reach the AVCN 2 ms after stimulating the ANF. Bürck and van Hemmen (2007) conclude that there is a very important function of the CN that appears to be *monaural echo suppression*.

Overview of numerical models of cell types in the cochlear nucleus

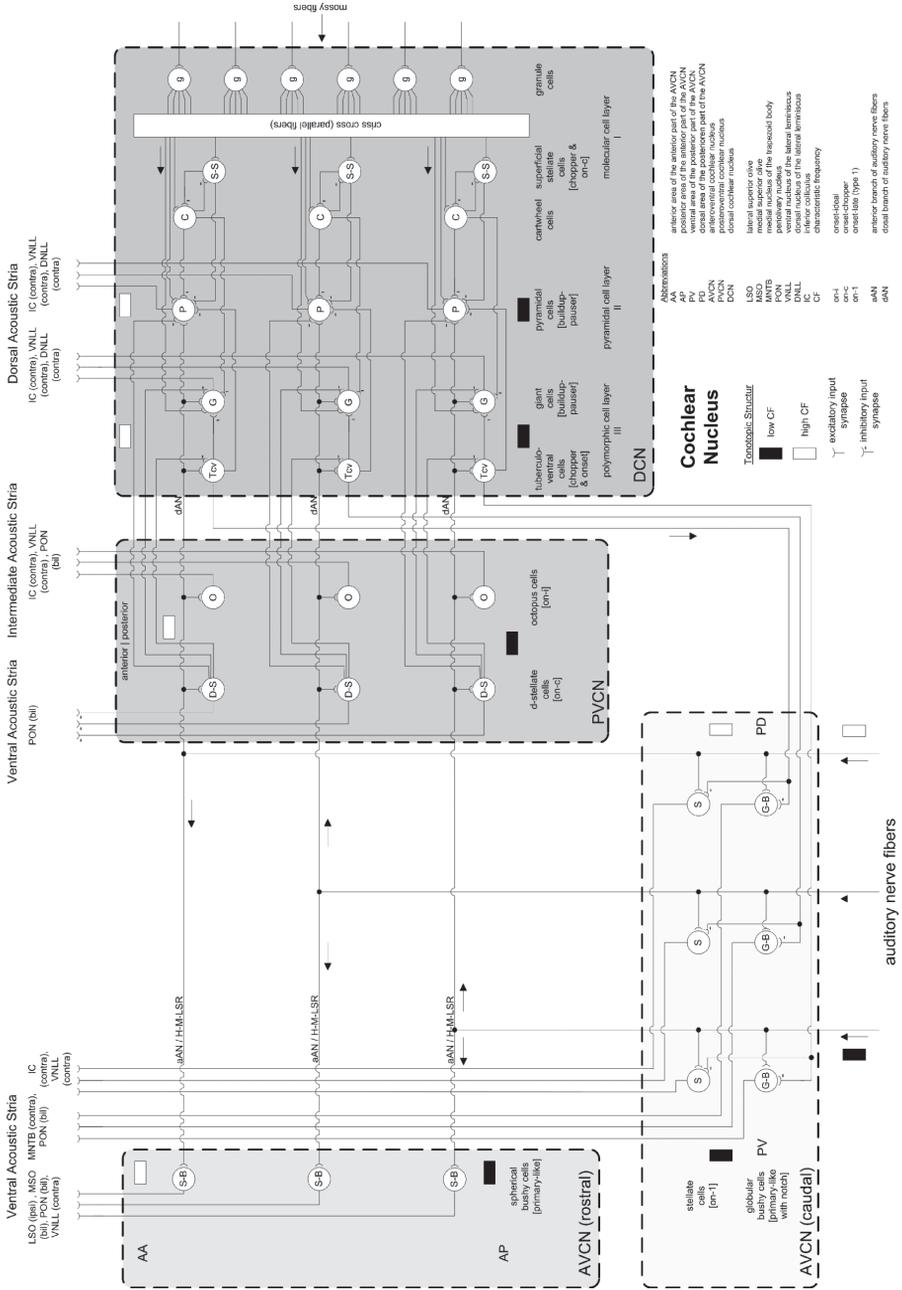


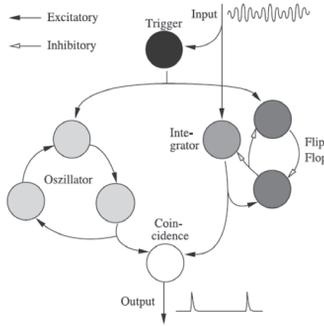
Fig. 2: Map of the cochlea nucleus; signal flow is shown for three auditory nerve fibers as input.

The outputs of the CN are innervating the superior olivary complex (SOC) and the inferior colliculus (IC) of the ipsi and contra lateral side. These regions are key areas for encoding binaural cues like interaural time (ITD) and level differences (ILD). The globular and spherical bushy cells in the AVCN have a more precise encoding of the acoustic waveform phase than the ANFs, which is helpful for sound source localization (Wittig jr., 2004; Louage *et al.*, 2005). The two CNs seemed to be *preprocessing stages for binaural cue extraction* (Ehret and Romand, 1997; Voutsas and Adamy, 2007). Oertel and Young (2004) describe that the inhibitory circuits between the giant and pyramidal cells in the DCN allows encoding peaks and notches in the spectra of sounds. Spectral notches can be caused by the head related transfer function and superimposed sound fields. They may be important for spatial encoding in the IC. Next to this, the DCN is also excited by multimodal inputs from higher regions of the brain. It can be supposed that these inputs are providing a kind of top-down information and may play a role in a schema-driven process.

### **Periodicity detection**

Wang and Brown (1999) built a computational neural model for segregating speech from interfering sound sources by an oscillatory correlation. One stage of their model is the estimation of the fundamental frequency by auto-correlation. Another feature is the periodicity and amplitude modulation of a sound signal, which is supported by Frisina *et al.* (1990). They do this by cross-correlation between adjacent auto-correlogram channels. Borst *et al.* (2004) and Voutsas *et al.* (2005) developed a biologically inspired model to extract the periodicity of complex sounds. They connect the signal processing of various neurons in the CN with neurons of the IC (Fig. 3).

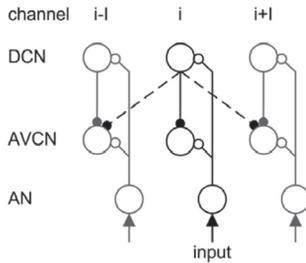
One modeled neuron is a trigger neuron, which conforms to onset behavior. In Fig. 2 it can be allocated with the d-stellate units in the PVCN, which show onset-chopper behavior. They forward their signal to several cells in the DCN. Other neurons are the oscillator neurons, which are triggered by d-stellate units. Borst *et al.* (2004) locate these neurons in the VCN as chopper neurons. But there is some evidence that, in this case, the mentioned units may be tuberculoventral cells in the DCN (Ehret and Romand, 1997). They are triggered by d-stellate units and show a chopper behavior. Further numerical models for representing periodic sounds are e.g. the simulation of chopper units in the VCN by Wiegrebe and Meddis (2004) and a model introduced by Friedel *et al.* (2007), which is based on the idea of delay lines to detect periodicities. Next to this, Kalluri and Delgutte (2003) modeled onset neurons in the PVCN and AVCN to understand their behavior as coincidence-detector. Onset behavior is very important to detect periodicities in a sound signal (Hemmert *et al.*, 2005), and to implement monaural auditory segmentation (e.g. Hu and Wang, 2004, 2007).



**Fig. 3:** Model from Borst *et al.* (2004).

**Monaural echo suppression**

Bürck and van Hemmen (2007) developed a mathematical model of the CN, which deals with inhibitory interconnections between DCN and AVCN (Fig. 4). This model gives the possibilities to implement a kind of gain control, contrast enhancement, and monaural echo suppression. In the map of the CN (Fig. 2) one can find the modeled neurons as tuberculoventral cells in the DCN and as globular bushy cells in the caudal part of the AVCN.



**Fig. 4:** Model from Bürck and van Hemmen (2007). Black circles are inhibitory synapses, white circles are excitatory synapses, dashed lines represent spreading of inhibition.

Other sources mention that the tuberculoventral units achieve additional inhibitory input from the d-stellate units in the PVCN (e.g. Oertel and Young, 2004). These units are assigned as trigger neurons, which are phase-coupled to the period of the envelope of the input signal (Borst *et al.*, 2004).

### **Preprocessing for binaural cue extraction**

Voutsas and Adamy (2007) developed a biologically inspired neural model for sound source localization based on delay lines in the sense of the Jeffress model. The estimation of the direction of arrival is done for interaural time and level differences. In their paper they describe the signal flow through the AVCN for ITD and ILD. The signals for ITD analysis go through the spherical bushy cells in AVCN to the medial superior olive (MSO). The globular bushy cells in the AVCN are involved in ILD analysis. The next signal processing step for ILDs is in the lateral superior olive (LSO). It has to be noted that the globular bushy units are also involved in the assumed monaural echo suppression described by Bürck and van Hemmen (2007), and in the periodicity detection described by Wang and Brown (1999).

Schauer *et al.* (2007) and Pecka *et al.* (2007) describe an approach for sound source localization which deals with signal processing in the IC. Schauer *et al.* (2007) assume that a sharpening of the tonotopic binaural feature representation is done by lateral interconnections, and a summation of the tonotopic representation is done in the IC. Pecka *et al.* (2007) expect that DNLL (dorsal nucleus of the lateral lemniscus) neurons generate a context-dependent suppression (persistent inhibition) of directional information. This may be in line with the encoding of spectral notches by DCN neurons.

### **CONCLUSION**

A map of the cochlear nucleus (CN) is build up from the literature of physiological and computational neurosciences. This map shows the principal structure, cell types, interconnections and output terminals from an engineering point of view. Some numerical models of auditory cue encoding are assigned to the different cell types of the CN. Some cue encoding models are described briefly which can be a starting point for further reading. An interesting field of research is the development of numerical models which incorporate information from higher regions of the brain like the head position or multimodal inputs for example. A challenging point is to verify if there is descending information that is comparable with schema-driven processes and to develop computational models of them. One candidate is maybe the encoding of spectral notches and the auditory perception in the superimposed sound field. Faller and Merimaa (2004) introduce such a motivated model for binaural sound source localization based on adaptive interaural coherence for example.

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